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Explanation of the bilateral deficit in human vertical squat jumping

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Bobbert, Maarten F., Wendy W. de Graaf, Jan N. Jonk, and L. J. Richard Casius. Explanation of the bilateral deficit in human vertical squat jumping. *J Appl Physiol* 100: 493–499, 2006. First published October 20, 2005; doi:10.1152/jappphysiol.00637.2005.—In the literature, it has been reported that the mechanical output per leg is less in two-leg jumps than in one-leg jumps. This so-called bilateral deficit has been attributed to a reduced neural drive to muscles in two-leg jumps. The purpose of the present study was to investigate the possible contribution of nonneural factors to the bilateral deficit in jumping. We collected kinematics, ground reaction forces, and electromyograms of eight human subjects performing two-leg and one-leg (right leg) squat jumps and calculated mechanical output per leg. We also used a model of the human musculoskeletal system to simulate two-leg and one-leg jumps, starting from the initial position observed in the subjects. The model had muscle stimulation as input, which was optimized using jump height as performance criterion. The model did not incorporate a reduced maximal neural drive in the two-leg jump. Both in the subjects and in the model, the work of the right leg was more than 20% less in the two-leg jump than in the one-leg jump. Peak electromyogram levels in the two-leg jump were reduced on average by 5%, but the reduction was only statistically significant in m. rectus femoris. In the model, ~75% of the bilateral deficit in work per leg was explained by higher shortening velocities in the two-leg jump, and the remainder was explained by lower active state of muscles. It was concluded that the bilateral deficit in jumping is primarily caused by the force-velocity relationship rather than by a reduction of neural drive.

inverse dynamics; simulation model; muscle excitation; force-velocity relationship; muscle work

IN SEVERAL STUDIES (4, 16, 19), it has been reported that, in a two-leg jump, humans achieve less than twice the jump height they are able to reach in a one-leg jump. The implication that the amount of work produced per leg in a two-leg jump is less than in a one-leg jump has been confirmed by inverse dynamics analysis (16). This finding is reminiscent of a phenomenon known as the bilateral force deficit: the maximum voluntary force produced by a subject with the muscles of one limb is less when these muscles are active simultaneously with the homologous muscles in the contralateral limb than when they are active alone. Following the first description of this phenomenon by Henry and Smith (8), numerous investigators have searched for a bilateral force deficit in isometric and isokinetic leg tasks and arm tasks (for review, see Ref. 11). Although most investigators have confirmed its existence (e.g., Refs. 13, 14), some investigators were unable to find a bilateral force deficit (10), and a few have even reported a bilateral facilitation (9). To explain these different findings, some of which were obtained in apparently similar tasks executed by apparently similar subjects, various factors have been proposed, such as

the level of training of the subjects and their familiarity with the task. To date, however, a conclusive explanation of the bilateral force deficit is still lacking.

If a bilateral deficit is found in isometric or isokinetic tasks, there is no alternative but to attribute it to a reduced neural drive to the muscles of the individual limbs when the task is executed bilaterally compared with when it is executed unilaterally (9, 13, 14). The lesser work per leg in a two-leg jump compared with a one-leg jump, however, is not necessarily due to a reduced neural drive. Even when the range of motion over which the joints extend is the same in both types of jumps, it will be obvious that at least some extensor muscles will reach higher shortening velocities in the two-leg jump, and due to the force-velocity relationship these muscles will tend to produce less force and less work than in the one-leg jump. Also, in the two-leg jump body weight is distributed over two legs so that the muscles of the individual legs will have a reduced active state in the equilibrium initial position; in other words, they are initially further away from their maximal active state in the two-leg jump than in the one-leg jump. Considering that it takes time to build up active state, it is plausible that in the two-leg jump the extensor muscles travel a greater part of their shortening range at submaximal active state and hence produce submaximal force and work. This latter factor will be more important when squat jumps are studied than when countermovement jumps are studied (2).

Authors of previous papers on the bilateral deficit in mechanical output per leg in two-leg and one-leg jumps were aware that factors other than neural drive could play a role. Van Soest et al. (16), studying two-leg and one-leg countermovement jumps, mentioned the possibility that the force-velocity relationship explained part of the bilateral deficit in mechanical output but discarded it after comparing qualitatively the shortening velocities of muscle-tendon complexes (MTCs) in the two-leg and one-leg jumps. Because they had found a lower electromyogram (EMG) level of some muscles in the two-leg jump, they concluded that the observed bilateral deficit in mechanical output was due to a reduction of neural drive in the two-leg jump. Challis (4), studying two-leg and one-leg squat jumps, investigated the possible role of both the force-velocity relationship and excitation dynamics using a simple simulation model of a jumper, actuated by knee extensors only. If the maximal neural drive to each leg in the model was fixed regardless of the type of jump, the maximal height reached in a simulated two-leg jump was twice the height reached in a simulated one-leg jump. From this, Challis also concluded that the bilateral performance deficit in jumping, which he had observed in his subjects, was due to a reduction of neural drive in the two-leg jump. He went on to speculate that this reduction of neural drive was related to the fact that, in the major ways of locomotion, humans use only one leg at a time for propelling body mass.

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Although the EMG results of the study of Van Soest et al. (16) suggest that the neural drive in a two-leg jump is indeed lower than in a one-leg jump, the contributions of nonneural factors to the bilateral deficit in jumping may have been discarded prematurely. Van Soest et al. (16) compared shortening velocities of MTCs in the two-leg and one-leg jump, but in fact it is the muscle fiber shortening velocities that affect the force produced by muscles, and in jumping the two may be very different (1, 12). Challis (4) only incorporated knee extensor muscles in his simulation model, but the bilateral deficit in mechanical output at the knee joint seems to explain only part of the total difference in mechanical output per leg between a two-leg jump and a one-leg jump (4, 16). Moreover, Challis (4) focused only on the vertical displacement of the center of mass in the airborne phase, which is not a good measure for the mechanical output of the muscles because it neglects the work done to raise the center of mass during the pushoff. We felt, therefore, that an in-depth analysis of the mechanical output in two-leg and one-leg jumps was required to determine the contributions of the force-velocity relationship and excitation dynamics to the bilateral deficit in jumping. The purpose of the present study was to conduct such an analysis. For this purpose, we had subjects perform two-leg and one-leg vertical squat jumps, and we also simulated these jumps with a realistic forward dynamic model of the human musculoskeletal system. The simulation results were used to examine the cause for the bilateral deficit in mechanical output.

MATERIALS AND METHODS

Subject experiments. Eight physically active male subjects, experienced in jumping because of their training background (volleyball or gymnastics), participated in this study. Informed consent was obtained from all of them in accordance with the policy statement of the American College of Sports Medicine. Characteristics of the group of subjects (means \pm SD) were: age 20 ± 4 yr, height 1.84 ± 0.09 m, and body mass 74.2 ± 15.4 kg. The subjects performed maximum-height squat jumps using either two legs or only the right leg for pushoff, while keeping their hands interlocked behind their back and the arms extended and in contact with their back. They were instructed to make no countermovement and, in the one-leg jump, to keep the left leg inactive under the body. After a number of practice trials, they were able to perform the jumps as required. In the actual experiment, each subject performed ~ 30 jumps in total, with two-leg and one-leg jumps alternating. Consecutive jumps were interspersed by 1-min rest intervals, which were sufficient to prevent the subjects from becoming fatigued. To ensure that the initial configuration of the right side of the body was the same in the two-leg and one-leg jumps, a body template was used consisting of rigid segments interconnected by hinge joints (3). This template was set to represent the right side of the body in the initial position that the subject preferred for the one-leg jump, and at the start of each two-leg jump the subject attempted to match his initial position to the configuration of the template. In the initial position that the subjects preferred for the one-leg jump after the practice trials, the knee angle was on average 122° (with 180° being full extension).

During jumping, ground reaction forces were measured with two force plates, sagittal-plane positional data of anatomical landmarks were collected, and EMGs were recorded from six muscles of the right lower extremity. Jump height, defined as the difference between the height of the center of mass of the body at the apex of the jump and the height of the center of mass when the subject was standing upright with heels on the ground, was calculated from the position data. The highest jump of each condition was selected for further analysis. Net joint moments and work of the individual legs were obtained by performing an inverse-dynamics analysis, combining kinematic infor-

mation and ground reaction forces. Differences between one-leg jumps and two-leg jumps were tested for statistical significance using a Student's *t*-test for paired comparisons. Details on experimental methods and procedures are provided below.

Ground reaction forces were measured using two force platforms (Kistler 9281B, Kistler Instruments, Amherst, NY). One platform measured the force of the right leg, the other platform measured in the two-leg jump condition also the force of the left leg. The output signals of the platforms were amplified (Kistler 9865E charge amplifier, Kistler Instruments), sampled at 200 Hz, and processed to determine the fore-aft and vertical components of the reaction force and the location of the center of pressure.

Kinematic data were collected using an Optotrak (Northern Digital, Waterloo, Ontario) motion-analysis system, operating at 200 Hz. Landmarks were placed on both sides of the body at the fifth metatarsophalangeal joint, calcaneus, lateral malleolus, lateral epicondyle of the femur, greater trochanter, and acromion. Only sagittal plane projections were used in this study. The time histories of marker positions were smoothed using a bidirectional low-pass Butterworth filter with a cutoff frequency of 16 Hz. The locations of the mass centers of upper legs, lower legs, and feet were estimated from the landmark coordinates, in combination with results of cadaver measurements presented in the literature (5). To determine the location of the mass center of the upper body relative to the two markers on this segment, the subject was asked to assume two equilibrium postures on tiptoes, one with the hip joints fully extended and one with the hip joints flexed. This yielded two equations for the fore-aft coordinate of the center of mass of the body, which in the case of equilibrium equals the fore-aft coordinate of the center of pressure on the ground, detected with the force plates. The two equations were solved for the two unknown coordinates of the center of mass of the upper body relative to the markers on this segment. With this information, the position of the center of mass of the body was calculated in all other body positions found during jumping. To obtain linear velocities and accelerations, the smoothed position time histories were differentiated numerically with respect to time using a direct five-point derivative routine. Angles of body segments with respect to the horizontal were calculated from the smoothed marker position time histories and differentiated to obtain angular velocities and accelerations.

Net intersegmental forces and moments were calculated by means of a standard inverse-dynamics analysis (16) using the measured ground reaction force vector, locations of joint axes and segmental mass centers obtained from the position data, linear and angular accelerations of segments derived from position data, segmental masses, and segmental moments of inertia calculated from these segmental properties using regression equations (20). Hip extension, knee extension, and plantar flexion moments were defined as positive.

To get an impression of muscle activation in the right leg, pairs of Ag/AgCl surface electrodes (Medicotest, blue sensor, type N-00-S) were applied to the skin overlying m. soleus, m. gastrocnemius (caput mediale), m. vastus lateralis, m. rectus femoris, m. gluteus maximus, and m. biceps femoris (caput longum). EMG signals were amplified and sampled at 1,000 Hz (Porti-17t, Twente Medical Systems). Offline, they were high-pass filtered (7 Hz) to remove any possible movement artifacts, full-wave rectified, and smoothed using a bidirectional digital low-pass Butterworth filter with a 7-Hz cutoff frequency to yield smoothed rectified EMG (SREMG).

Computer simulations. For simulations of jumps, we used a two-dimensional forward dynamic model of the human musculoskeletal system. The model, which had muscle stimulation as its only independent input, consisted of seven rigid segments representing right foot, right shank, right thigh, left foot, left shank, left thigh, and a head-arms-trunk segment. These segments were interconnected by hinge joints representing hip, knee, and ankle joints, and the distal part of the foot was connected to the ground in a hinge joint. In the initial configuration, the rotational degree of freedom of the foot was fixed to mimic that the subjects had their heels on the ground, and we

calculated the moment of the ground reaction force relative to the distal part of the foot that was needed to prevent angular acceleration of the foot. The rotational degree of freedom was released during simulations when the calculated moment of the reaction force dropped to zero. Segment parameters were the same as those used in a model for simulation of two-leg jumping, which was previously described in full detail (17). In the skeletal submodel, 15 major MTCs of the lower extremity were embedded: hamstrings (their biarticular heads), m. gluteus maximus, m. rectus femoris, vasti, m. gastrocnemius and m. soleus of both legs, and additionally in the left leg m. iliopsoas, short head of m. biceps femoris, and m. tibialis anterior. Each MTC was represented using a Hill-type muscle model. This muscle model, which has also been described in full detail elsewhere (18), consisted of a contractile element (CE), a series elastic element, and a parallel elastic element. Briefly, behavior of series elastic element and parallel elastic element was determined by a quadratic force-length relationship. Behavior of CE was more complex: CE velocity depended on CE length, force, and active state (g), with the latter being defined as the relative amount of calcium bound to troponin (6). Active state was not an independent input of the model but was manipulated indirectly via muscle stimulation (STIM). Following Hatze (7), the relationship between active state and STIM was modeled as a first-order process. STIM, ranging between 0 and 1, was a one-dimensional representation of the effects of recruitment and firing frequency of α -motoneurons.

At the start of each simulation, the model was put in an initial position derived from the subject experiments, and the initial STIM levels were set in such a way that the net joint moments kept the system in static equilibrium. To find a unique solution for the initial STIM levels, we first assigned a STIM level of 0.01 to the biarticular hamstrings, rectus femoris, and gastrocnemius, causing them to produce a small force that took up the slack in series elastic element. Subsequently, we calculated the STIM levels for the other muscles that ensured equilibrium of the system as a whole. During propulsion in the two-leg jump, STIM of each muscle was allowed to increase from its initial level toward its maximum of 1. The increase started at a switch time and occurred at a fixed rate of 2.2 s^{-1} ; it was shown previously that if STIM was increased at this rate,

the rate of change of the ground reaction force in two-leg squat jumps of human subjects was satisfactorily reproduced with the model (2). In the one-leg jump, only the STIMs of the muscles of the right leg were allowed to change from their initial level to the maximum; the STIMs of the muscles of the left leg were kept at the level required to hold the leg suspended in equilibrium. Under these restrictions, the motion of the body segments, and therewith performance of the model, depended on a set of switch times. Thus an optimization problem could be formulated: finding the combination of switch times that produced the maximum value of the height achieved by the center of mass of the body and thereby maximum jump height. The optimization problem was solved using a genetic algorithm (15). For each condition, the optimization ran for 1,000 generations of a population of 100 chromosomes, with each chromosome being a bit string coding a combination of stimulation onset times at 1-ms resolution.

Once the solutions were found for the maximum-height two-leg and one-leg jumps, we used them to determine the cause for differences in muscle work performed. Muscle work is the integral of muscle force with respect to length of the MTC, with muscle force depending on CE length, CE velocity, and active state. We estimated the effect of differences in CE velocity between the two types of jumps by substituting at each MTC length in the two-leg jump the CE velocity at the same MTC length in the one-leg jump, which was found using interpolation. With the original active state and CE length of the two-leg jump and the substituted CE velocity of the one-leg jump, we then recalculated muscle force and integrated the newly obtained force with respect to MTC length to obtain a corrected work output. We also estimated the additional effect of differences in active state between the two types of jumps by subsequently substituting at each MTC length in the two-leg jump both the CE velocity and the active state at the same MTC length in the one-leg jump, and recalculating muscle force and work.

RESULTS

Figure 1 presents average stick diagrams of the subjects at different instants during the two-leg and one-leg jumps, Fig. 2

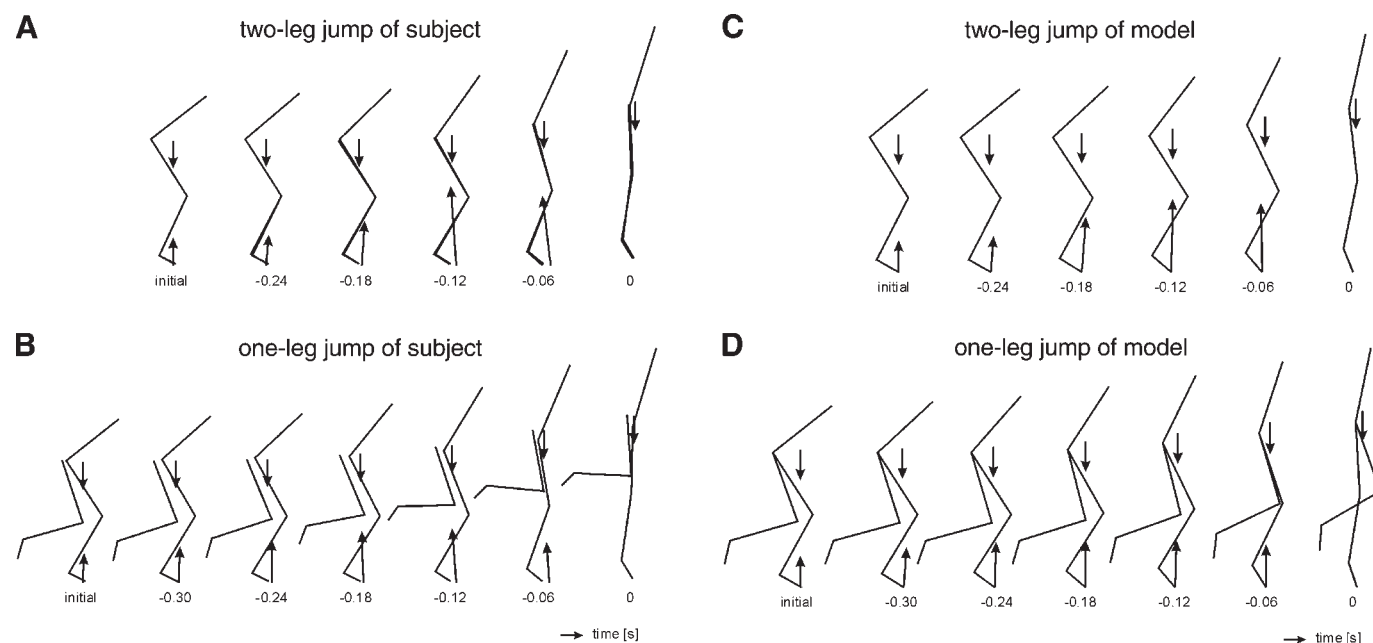


Fig. 1. Stick diagrams of average body positions of the 8 subjects (A and B) and the simulation model (C and D) for the pushoff in two-leg and one-leg jumps. Arrows pointing upward represent the ground reaction force vector plotted with the origin in the center of pressure; arrows pointing downward represent the force of gravity, plotted with the origin in the center of mass. Time is expressed relative to the instant of takeoff (time = 0). It should be pointed out that the duration of the pushoff was less in the two-leg jump than in the one-leg jump. In the subjects, the average pushoff time was 261 ms in the two-leg jump and 372 ms in the one-leg jump. In the simulation model, the duration of the pushoff was 265 ms in the two-leg jump and 406 ms in the one-leg jump.

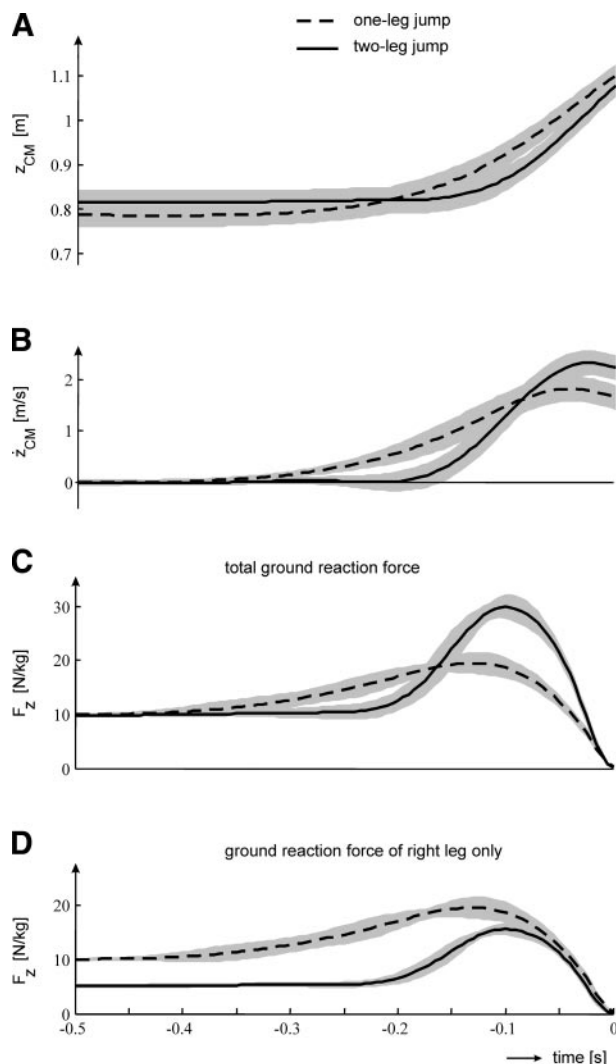


Fig. 2. Time histories of the height of the center of mass (z_{cm}) (A), rate change of the z_{cm} (B), total vertical ground reaction force (F_z) (C), and F_z of the right leg (D) of the subjects during the two-leg and one-leg jumps. Time is expressed relative to the instant of takeoff (time = 0). Curves represent means \pm SD (gray areas) of the subjects ($n = 8$).

shows time histories of variables related to the motion of the center of mass, and Table 1 lists the values of selected parameters describing the performance in the jumps. At first glance, the initial configuration of the body was quite similar in the two types of jumps (Fig. 1). On closer inspection, however, the height of the center of mass was ~ 3 cm less at the start of the one-leg jump (Fig. 2A), because the subjects had their joints on average slightly more flexed in the one-leg jump than in the two-leg jump (Fig. 1). At takeoff, the height of the center of mass was ~ 2 cm greater in the one-leg jump (Fig. 2A) because the subjects rotated the pelvis in the frontal plane (Fig. 1) causing the left side of their body to be raised. The total change in mechanical energy of the center of mass during the push off was 4.9 J/kg in the two-leg jump and 4.3 J/kg in the one-leg jump (Table 1). Clearly, the total change in mechanical energy in the two-leg jump was less than twice that in the one-leg jump. The total change in mechanical energy is equal to the surface under the curve obtained when the ground reaction force is plotted as a function of the displacement of the center

of mass during the push off, as was done in Fig. 3B. The surface in the two-leg jump is less than twice that in the one-leg jump, partly because the range of motion was smaller but primarily because the ground reaction force was less than twice that in the one-leg jump over most of the range of motion (Fig. 3B); the right leg produced less force in the two-leg jump than in the one-leg jump (Fig. 3C), but obviously the velocity of the center of mass was greater over most of the range of motion in the two-leg jump (Fig. 3A). The peak vertical ground force of the right leg attained in the two-leg jump (15.6 ± 1.1 N/kg) was slightly larger ($P < 0.05$) than that of the left leg (14.2 ± 1.2 N/kg), implying right-leg dominance for the group of subjects. This did not bias the comparison between the two-leg and one-leg jumps because the experimental setup allowed us to determine directly the mechanical output of the right leg in both types of jumps.

In the two-leg jump, the total change in mechanical energy could be fully explained by the total joint work produced during the pushoff phase as obtained by the inverse dynamics analysis, which was 2.6 J/kg for the right leg (Table 1) and 2.5 J/kg for the left leg (not shown), giving a total work output of 5.1 J/kg. [It should be taken into account that part of the work produced flows to ineffective energy, such as rotational energy of segments, which is dissipated in the airborne phase; in simulated jumps, the ineffective energy at takeoff amounts to 13% of the total work produced (17).] This indicates that the calculation of work produced at the ankle, knee, and hip joints was valid. In the one-leg jump, the total change in mechanical energy could not be fully explained by the total joint work produced during the pushoff phase (Table 1), primarily because the work of the right hip abductors, responsible for the rotation of the pelvis in the frontal plane, was not taken into account. Total joint work calculated for the right leg in the two-leg jump was only 78% of that in the one-leg jump because work at the knee and ankle of the right leg in the two-leg jump was reduced substantially compared with the one-leg jump. The deficit in joint work produced by the right leg in the two-leg jump compared with the one-leg jump was primarily due to a deficit in joint moments. An impression of this deficit can be gained from the peak joint moments. For example, the peak extension moment at the knee of the right leg in the two-leg jump was 58% of that in the one-leg jump, and for the peak plantar flexion moment this value was 80%. Peak SREMG levels achieved during the pushoff in the two-leg jump, expressed as fraction of those achieved in the one-leg jump, were 0.94 ± 0.19 for m. soleus, 0.93 ± 0.17 for m. gastrocnemius, 0.91 ± 0.14 for m. vastus lateralis, 0.88 ± 0.12 for m. rectus femoris, 1.01 ± 0.32 for m. gluteus maximus, and 1.02 ± 0.29 for m. biceps femoris. Only for m. rectus femoris was this fraction significantly different from 1 ($P < 0.05$). When averaged over all muscles and subjects, the peak SREMG level achieved during the push off in the two-leg jump, expressed as fraction of that achieved in the one-leg jump, was 0.95.

Figure 1, C and D, presents stick diagrams of the model at different instants during the simulated two-leg jump and one-leg jump, respectively, and Table 1 lists the values of selected parameters describing the performance. Overall, the correspondence between the simulated jumps and the subject jumps was quite satisfactory. The total change in mechanical energy of the center of mass was 4.6 J/kg in the two-leg jump and 3.4 J/kg

Table 1. Selected parameters describing the performance in the two-leg and one-leg jumps of the subjects and of the model

Variable	Unit	Joint	Simulation Model		Two-leg jump	One-leg jump
			Two-leg jump	One-leg jump		
$t_{\text{push-off}}$	s		0.261 ± 0.065	$0.372 \pm 0.048^*$	0.265	0.406
$z_{\text{CM,start}}$	m		-0.212 ± 0.054	$-0.241 \pm 0.068^*$	-0.182	-0.183
$z_{\text{CM,to}}$	m		0.046 ± 0.019	$0.068 \pm 0.038^*$	0.062	0.079
$z_{\text{CM,max}}$	m		0.283 ± 0.060	$0.193 \pm 0.051^*$	0.284	0.162
ΔE_{mech}	J/kg		4.86 ± 1.05	$4.26 \pm 0.93^*$	4.57	3.38
$F_{z,\text{max}}$ of RL	N/kg		15.6 ± 1.1	$19.6 \pm 2.1^*$	11.9	15.1
M_{max} of RL	Nm/kg	hip	1.67 ± 0.40	$2.18 \pm 0.28^*$	1.85	2.69
		knee	1.63 ± 0.27	$2.24 \pm 0.34^*$	1.26	1.73
		ankle	2.27 ± 0.15	$2.62 \pm 0.21^*$	1.53	2.03
Joint work of RL	J/kg	hip	0.75 ± 0.33	0.79 ± 0.30	1.08	1.69
		knee	0.55 ± 0.21	$0.87 \pm 0.26^*$	0.72	1.06
		ankle	1.26 ± 0.14	$1.61 \pm 0.17^*$	0.87	1.29
Total work of RL	J/kg		2.56 ± 0.51	$3.27 \pm 0.51^*$	2.67	4.03

Values are means \pm SD; $n = 8$. $t_{\text{push-off}}$, Pushoff duration, defined as the time interval between the instant that the total vertical ground reaction force increased above 105% of body weight and the instant of takeoff; $z_{\text{CM,start}}$, height of the center of mass of the body at the start of the jump relative to standing upright; $z_{\text{CM,to}}$, height of the center of mass of the body at takeoff relative to standing upright; $z_{\text{CM,max}}$, height of the center of mass of the body at the apex of the jump relative to standing upright; ΔE_{mech} , change in mechanical energy of the center of mass from start to take-off; $F_{z,\text{max}}$ of RL, peak vertical ground reaction force of the right leg; M_{max} of RL, peak net joint moment produced at the different joints of the right leg; Joint work of RL, net joint work produced at the different joints of the right leg; Total work of RL, sum of the work of the individual joints of the right leg. *Difference between the two-leg jump and one-leg jump was statistically significant ($P < 0.05$).

in the one-leg jump, and total work produced per leg during the propulsion phase in the two-leg jump was only 68% of that produced in the one-leg jump. The work done during the propulsion phase is the sum of the work produced by the individual muscles, presented in Table 2. The work produced

by each individual muscle is equal to the integral of force with respect to MTC length, with force depending on CE length, CE contraction velocity, and active state. In the two-leg jump, peak CE shortening velocities were higher and active state values were initially lower in the two-leg jump than in the one-leg jump. This is illustrated in Fig. 4 for one muscle, m. soleus of the right leg. This muscle was selected for illustration because it is the major contributor to ankle joint work, with the latter being substantially lower in the two-leg jump than in the one-leg jump, both in the simulations and in the subjects (Table 1). As explained before, to estimate the extent to which the higher shortening velocities in the two-leg jump contributed to the work deficit, we substituted for each muscle at each MTC length in the two-leg jump the shortening velocity at the same MTC length in the one-leg jump and subsequently recalculated muscle force and work. This caused total muscle work of the

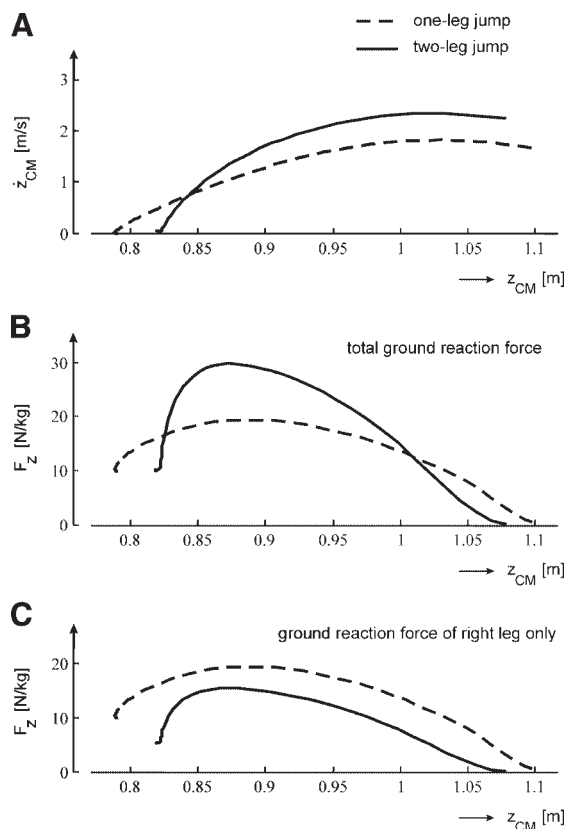


Fig. 3. Vertical velocity of the center of mass (A), total F_z (B), and F_z of the right leg (C) of the subjects during the two-leg and one-leg jumps plotted against the z_{CM} . Curves represent mean values of the subjects ($n = 8$).

Table 2. Work (in J/kg) produced by the model's MTCs of the right leg during the propulsion phase in the two-leg and one-leg jumps

	Two-Leg Jump	Two-Leg Jump Correction V_{CE}	Two-Leg Jump Correction V_{CE} and q	One-Leg Jump
Hamstrings	0.46	0.64	0.73	0.70
Gluteus maximus	0.88	1.13	1.31	1.30
Rectus femoris	0.02	0.05	-0.11	0.05
Vasti	0.55	0.82	0.85	0.84
Gastrocnemius	0.31	0.41	0.44	0.43
Soleus	0.46	0.67	0.78	0.70
Total	2.67	3.71	4.00	4.03

Work is the integral of force with respect to MTC length. We estimated the effect of the higher shortening velocity in the two-leg jump compared with the one-leg jump by substituting at each muscle-tendon complex (MTC) length in the two-leg jump the shortening velocity occurring at the same MTC length during the one-leg jump and recalculated work (correction V_{CE}). Next, we estimated the additional effect of the lower active state in the two-leg jump by substituting both the shortening velocity and the active state of the one-leg jump (correction V_{CE} and q).

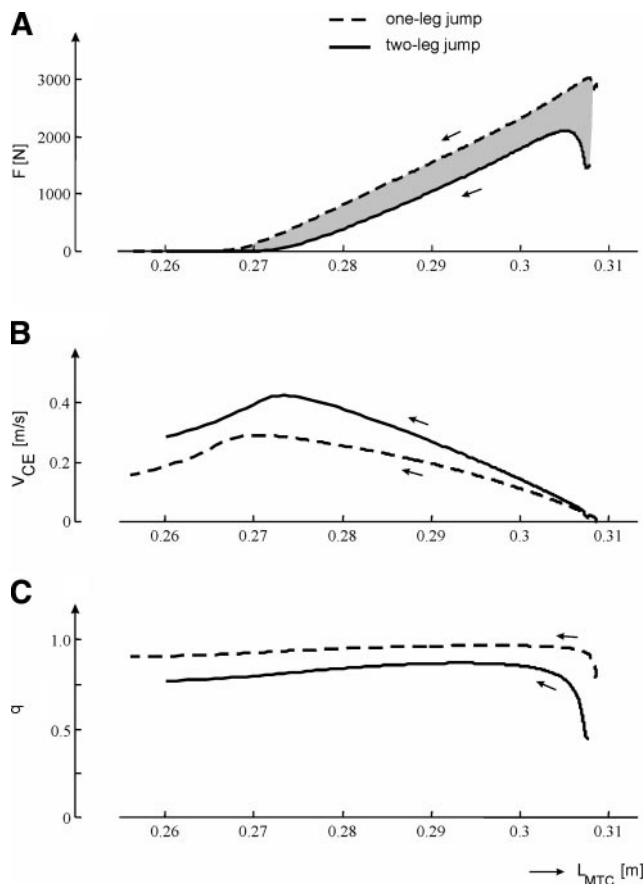


Fig. 4. Force (F), shortening velocity of contractile elements (V_{CE}), and active state (q) of m. soleus of the right leg as a function of MTC length (L_{MTC}) for the two-leg jump and the one-leg jump of the model. Arrows give the direction of time. Shaded area represents the surplus of work output of m. soleus of the right leg in the two-leg jump compared with the one-leg jump.

right leg in the two-leg jump to increase by no less than 1 J/kg, which was $\sim 75\%$ of the difference in work of the right leg between the two-leg and the one-leg jump (Table 2). Adding a similar correction for active state caused a further increase by 0.3 J/kg (Table 2). With these two corrections, the work deficit in the two-leg jump had disappeared (Table 2).

DISCUSSION

In the literature, the mechanical output per leg has been reported to be less during a two-leg jump than during a one-leg jump (4, 16). The purpose of this study was to explain this finding by performing an in-depth analysis of the mechanical output in two-leg and one-leg jumps performed by subjects as well as that in two-leg and one-leg jumps simulated with a forward dynamic model of the musculoskeletal system. Below, we shall first address the experimental results and then the simulation results.

In the literature, considerable attention has been paid to the observation that jump height in two-leg jumps is less than twice that achieved in the one-leg jumps (4, 16, 19). The ratio of jump heights is not very informative, however, because it depends strongly on whether jump height is defined relative to the height in upright standing (16) or whether it is defined relative to the height at takeoff (4). As a matter of fact, it would

be most straightforward to look at jump height relative to the bottom of the squat. After all, if muscle force depended only on neural drive and if the range of motion were the same, a subject would produce twice the muscle work pushing off with two legs instead of one, and if all muscle work was converted into potential energy, the subject would therefore realize twice the vertical displacement from the bottom of the squat to the apex of the jump in the two-leg jump compared with the one-leg jump (the vertical displacement of the center of mass after takeoff in the two-leg jump would even be more than twice that in the one-leg jump). In reality, the change in mechanical energy of the center of mass during the pushoff in the two-leg jump, and the corresponding total vertical displacement, did not attain 200% but only 114% of their values during the one-leg jump (Table 1), and the work per leg in the two-leg jump was not 100% but only 78% of that in the one-leg jump (Table 1). Following Challis (4), it was attempted to keep the range of motion the same in the two types of jumps, but we nevertheless ended up with a smaller vertical displacement of the center of mass during the pushoff in the two-leg jump than in the one-leg jump (Fig. 2A, Table 1). Needless to say, this unintentional difference in range of motion during the pushoff disfavors work production in the two-leg jump and therefore biases the comparison of two-leg and one-leg jumps. However, the smaller range of motion during the pushoff was only a secondary explanation for the reduced work per leg in the two-leg jump. The primary explanation was that the force produced by the individual legs was less in the two-leg jump than in the one-leg jump (Figs. 2D and 3C), which in turn was due to smaller (peak) joint moments (Table 1).

In principle, the joint moments in the two-leg jump could be smaller than those in the one-leg jump because of reduced neural drive. On average, the peak SREMG levels in the two-leg jump were indeed reduced in the two-leg jump compared with the one-leg jump, but the reduction was very small ($\sim 5\%$ when averaged over all muscles) and only statistically significant in m. rectus femoris. These findings are different from those of Van Soest et al. (16), who reported 10–20% lower SREMG activity of vastus medialis and gastrocnemius during push off in two-leg countermovement jumps compared with one-leg countermovement jumps. Perhaps the difference in outcome has to do with the averaging of SREMG over the pushoff phase by Van Soest et al. (16) and thereby the incorporation of a time interval in which the muscles were not yet fully activated. This might lead to a different result than using peak SREMG levels, because at the start of a one-leg jump the leg used for push off supports full body weight, whereas at the start of a two-leg jump each leg supports only half of body weight. In any case, it seems unlikely that the 20–30% bilateral deficit in peak joint moments found in the present study (Table 1) was explained by the relatively small differences in neural drive (as judged from peak SREMG-levels). More likely, the reduction of moments in the two-leg jump compared with the one-leg jump was due to differences in contractile conditions of the muscles. Because the velocity of the center of mass was greater in the two-leg jump than in the one-leg jump over most of the range of motion (Fig. 3A), at least some extensor muscles will have shortened at higher velocities in the two-leg jump and hence produced lower forces due to the force-velocity relationship. Also, in the two-leg jump, body weight was distributed over two legs, so that in the equilibrium initial

position the muscles of the individual legs will have had about half the active state and, because of limitations in the rate of increase of neural input and active state, will also have had a reduced active state over the first part of the range of shortening (this is illustrated for m. soleus of the model in Fig. 4C).

On the basis of the data collected in the experiments with the subjects, we obviously cannot quantify the contribution of differences in contractile conditions to the reduced work per leg in the two-leg jump compared with the one-leg jump. For this reason, we turned to simulations of these jumps with a model of the musculoskeletal system that has been shown to capture the characteristics of the real system that are salient for two-leg squat jumping (17) and two-leg countermovement jumping (2). Overall, a satisfactory correspondence was obtained between the simulated jumps and the jumps performed by the subjects (Fig. 1). The difference in jump height between the two-leg jump and the one-leg jump was ~ 3 cm greater in the model than in the subjects, but this was not surprising because contrary to the subjects the model did not benefit in the one-leg jump from a lower starting height of the center of mass and rotation of the pelvis in the frontal plane. Just like in the subjects, the work per leg was less in the two-leg jump than in the one-leg jump (Table 1), despite the fact that in the simulation model no deficit in maximal neural drive was incorporated. The outcome of the simulations did allow us to quantify the effect of differences in contractile conditions to the reduced work per leg in the two-leg jump compared with the one-leg jump. By substituting for each muscle at each MTC length in the two-leg jump the state of the muscle at the same MTC length in the one-leg jump and subsequently recalculating muscle work, we were able to show that muscle shortening velocity was by far the most important factor: the fact that shortening velocities were higher in the two-leg jump than in the one-leg jump (shown for m. soleus in Fig. 4B) explained $\sim 75\%$ of the deficit in the work per leg (Table 2). The remainder of the deficit could be explained by a reduced active state in m. soleus (Fig. 4C) and m. gluteus maximus over most of the shortening range in the two-leg jump, as evidenced by the nearly complete disappearance of the work deficit after additional correction for active state (Table 2).

In summary, the subjects showed a substantial deficit in mechanical output per leg in two-leg jumping compared with one-leg jumping, but the EMG results suggested that there was at best a minimal reduction of neural drive. The simulation model, in which no difference in maximal neural drive was incorporated, also showed a substantial deficit in mechanical output per leg in two-leg jumping compared with one-leg jumping. About 75% of the deficit in work per leg in the model could be explained by the difference in contraction conditions of muscles: in the two-leg jump, muscles traveled their range of shortening at greater speed and, because of the force-velocity relationship, produced less force. The remainder was explained by the fact that active state was lower in the two-leg jump than in the one-leg jump initially and over the first part of the range of shortening. If we accept the model as a realistic representation of the real system, the inevitable conclusion is that the bilateral deficit in jumping is primarily caused by the

force-velocity relationship rather than by a reduction of neural drive. This conclusion is different from that drawn by Challis (4), but his findings were basically the same and he would have come to the same conclusion as we have, had he not focused on the vertical displacement in the airborne phase but on the total work produced.

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